Isonome Mapping: Graphic Analysis of Patterns of Species Distribution

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Fine scale analysis of species distribution and abundance is important in understanding processes of vegetation change. A novel mapping technique based on simple quadrat-sampling was devised in 1941 for this purpose and used to describe and analyse the structure and patterns of species distribution in two vegetation types on Hawkesbury sandstone of the Hornsby Plateau. In moist shrubland and in the understorey of adjacent *Eucalyptus* woodland at two sites, relative densities of shrubby species were calculated from the total numbers of plants of individual species recorded in rectangular (9.1 x 0.9 m) quadrats arranged in a grid. For each species with a sufficiently high density, the variation in its relative density across the grid was mapped as contour lines of equal percentage value called 'isonomes' (from *iso*, equal, and *nome*, distribution). In isonome maps for individual species, mostly complex systems of isonomes with one or more centres of high relative density emerged. By superimposing isonome maps of individual species, the composite pattern of species distribution over the area revealed a complex social structure in which the centres of high relative density formed a mosaic, around the margins of which there was overlapping of the lower-value isonomes. Graphic analysis by isonome mapping has provided information on sandstone vegetation not previously reported: e.g. sociology of woodland and scrub communities, patterns of occurrence and density of species across sharp ecotones, and specific patterns have generated an hypothesis of temporal change operating at a small scale. In the application of isonome mapping techniques to other vegetation types, the investigator has to choose the appropriate size and spacing of the rectangular quadrats, so that variation in relative density of species across the grid will generate discernible patterns. This paper is of historic interest, not only as the first quantitative method devised to show the pattern of species distribution and abundance in a community, but also as the first quantitative analysis of sandstone vegetation. It is also a record of species composition of pristine communities, devoid of introduced species, in urban fringe, pre-development vegetation of Sydney.

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Introduction

The twentieth century has seen the evolution of new methods and techniques for the classification, description and quantitative analysis of vegetation.

The basis of quantitative investigations in plant sociology is the quadrat method, originally proposed for pastures by Stapledon (1912). Statistical methods of analysis gave information on the floristic composition of the community, or on density and type of distribution of species (random, over- and under-dispersion). With random dispersion, ecologists and agronomists had a valuable tool for studying changes in plant populations (Blackman, 1935; Ashby, 1935; Clapham, 1936).

The arrival of Ashby in 1938, as Professor of Botany at Sydney University, and his fascination with the complexity of sandstone vegetation stimulated studies by Beadle in arid western NSW and that of Pidgeon on the sandstone vegetation. It also led to the collaboration with Pidgeon (now I.M. Brewer) in 1939 in a rigorous statistical analysis (using random-sampling techniques and rectangular strip-quadrats) of the effects of over-grazing on vegetation around Broken Hill (Pidgeon and Ashby, 1940).

Further investigations planned in applied ecology (see Pidgeon & Ashby, 1940) were relinquished when Ashby established and directed the Australian Liaison Bureau to maximize science in the war effort, and the Botany Department began its co-operation with the CSIR (later CSIRO) Food Preservation Research Laboratory which involved some of the teaching and research staff in solving problems related to fruit storage and marketing.

The complex Hawkesbury sandstone vegetation had not been analysed by quantitative techniques prior to 1941, as until then there was no quantitative method whereby the structure or pattern of a community could be determined. In 1941, Ashby and Pidgeon devised a novel 'isonome' mapping technique, based on simple quadrat sampling in grids, to record patterns of distribution and abundance of species. It was used in 1941 by Pidgeon on Hawkesbury sandstone and sand dune vegetation. The technique was first outlined by Pidgeon and Ashby (1942), but the data have been recorded only in the D.Sc. thesis (Pidgeon, 1942), and have not been explored, expanded, or related to information since published on the flora of the central coast, NSW.

From the 1950's, different approaches to describing and analysing vegetation were developed: objective methods (Goodall, 1961), and quantitative techniques (Grieg-Smith, 1983). Ordination (Bray & Curtis, 1957) was followed by computer-based methods of association analysis (Williams & Lambert, 1959, and others) and multivariate analysis (Gauch, 1982; James & McCulloch, 1990). These powerful and sophisticated techniques are now used almost exclusively in analysis of vegetation.

The research described in this paper was done more than fifty years ago, during tenure (1937-41) of a Linnean Macleay Fellowship at the University of Sydney. The war and other priorities interrupted the publication of a number of quantitative studies in the thesis (Pidgeon, 1942).

Data on isonome mapping of sandstone vegetation might well have been left buried in the thesis, but for a number of reasons it is offered for publication. It is a contribution of historical interest, not only as the original quantitative method devised to analyse the structure and pattern of species distribution and abundance in a plant community, but also as the first quantitative analysis of plant communities on Hawkesbury sandstone. There was a lapse of thirty years before other quantitative studies, using computer-analysis, of the vegetation of the central coast of NSW were published: Siddiqi *et al.* (1972), Burrough *et al.* (1977), Buchanan & Humphreys (1980).

Another motive for offering this paper is the historic aspect of the data. Plant communities like species, can become endangered. With the spread of urbanisation, this has indeed happened to many communities on Hawkesbury sandstone, which, like the two sites investigated in 1941, are now lost to streets and housing. The complete floristic composition of these communities, given in the Appendix (a total of 110 species, including densities) provide a record of typical urban fringe sandstone communities in the 1940s, prior to development. The species composition of these pristine communities, particularly the absence of introduced species now common in urban fringe vegetation, is remarkable.

This paper also re-evaluates the isonome mapping technique, which although superseded by other techniques using computer-analysis, nevertheless has some intrinsic merits. The technique may interest ecologists who wish to summarize, in a simple way, the sociology of plant communities. By examining the vividly descriptive isonome maps, ecologists can readily obtain information on distribution and abundance of species, often more rapidly than from computer analysis. Isonome mapping may also reveal graphic evidence of temporal change, as in the analysis of sandstone vegetation, where some shrub species, abundant in scrub, were present in woodland as isolated, low-value isonomes, interpreted as 'relics'.

Analysis of patterns of species distribution and abundance may point to important ecological processes operating at small scales, e.g. changes in local density and distribution of obligate-seeder woody shrubs in relation to fire history (R. Whelan pers. comm.). As patterns are not always apparent by inspection, techniques for quantifying fine-scale patterns in vegetation are needed. Isonome mapping is one simple technique of those available to ecologists.

Previous studies of the vegetation of the central coast of New South Wales have been largely in terms of its variation across a range of habitats (Pidgeon 1937, 1938, 1940, 1941, 1942; Davis 1936, 1941; Siddiqi *et al.* 1972; Burrough *et al.* 1977; Buchanan 1980; Buchanan and Humphreys 1980; Outhred *et al.* 1985; Thomas and Benson 1985).

Locality Description

Terrain and Soils

Two sites were selected on Hawkesbury Sandstone in the south-eastern portion of the uplands of the Hornsby Plateau (Fig. 1), the boundaries of which are described by Bembrick *et al.* 1980.

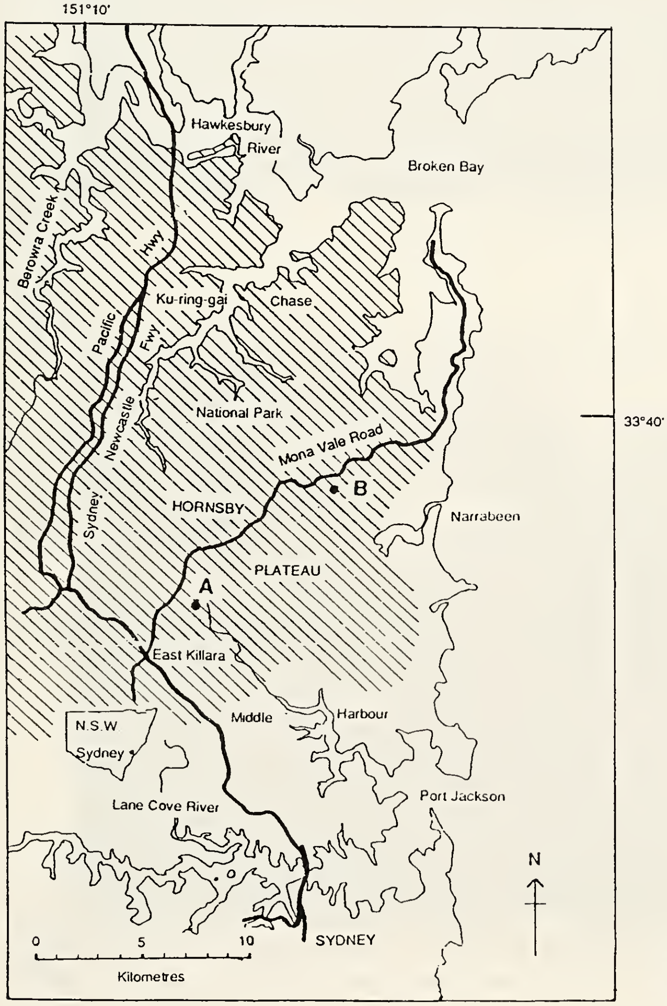

Fig. 1. Location of Sites A and B in the south-eastern section of the Hornsby Plateau.

The plateau, of fairly uniform elevation (180-210m ASL), is composed mainly of Hawkesbury Sandstone, a highly cemented and indurated quartz sandstone with thin interbedded shales and pebble lenses (Standard, 1969). The terrain of flat-topped divides and V-shaped valleys is typified by structural benches and a blocked and stepped appearance, resulting from the coarse jointing and horizontal bedding of the sandstone (Healy, 1972). Some sandstone strata and their intercalated shales are relatively impervious (Corbett, 1972). Where these underlie slopes of low angle, drainage is poor or impeded, thus determing the type of vegetation.

Soils derived from Hawkesbutry Sandstone are low in nutrients, especially phosphorus (Beadle, 1962) and nitrogen (Hannon, 1956) and range on the plateau from light-textured sandy lithosols to yellow podzolics, with discontinuous patches of acid peats.

Vegetation

The structural and floristic range of the vegetation of the plateau has been described previously by Pidgeon, (1938, 1940); Buchanan, (1980); Buchanan and Humphreys, 1980; Outhred *et al.,* (1985); Thomas and Benson, (1985).

The vegetation of the plateau is predominantly dry sclerophyll woodland with an open canopy (Beadle and Costin, 1952; Specht, 1970), mainly of *Eucalyptus* spp. and shrublands dominated by sclerophyllous shrubs, many of which also occur in the understorey of adjoining woodlands.

Differences in lithology, micro-topography, drainage and soils determine the distribution of two main types of shrubland: dry and moist scrub (Pidgeon, 1938). Dry scrub is found mainly on well drained skeletal soils, resting on sandstone close to the surface. Moist scrub occurs in habitats with impeded drainage, caused by impervious beds of massive sandstone or impervious sub-soils weathered from shale lenses. The soils are intermittently moist, occasionally water-logged but the surface is sandy without much organic matter (Pidgeon, 1938). Sometimes perched on benches, the majority of moist scrubs are found in areas of low slope (Buchanan, 1980). The dominance of indicator species, mainly moisture-tolerant shrubs especially *Hakea teretifolia*, readily identify these communities.

Many shrubs are common to both dry and moist scrub (Pidgeon, 1938) and the two communities may be in proximity (see Fig. 2).

Study Sites

A characteristic feature of the sandstone uplands is the recurring pattern of *Eucalyptus* woodland on well-drained soils interspersed with areas of moist scrub. In these adjacent communities, two sites of apparently similar floristic composition were selected for quantitative analysis: Site A, at east Gordon, and Site B, about 10 km to the east in the vicinity of Elanora Heights (Fig. 1). Selected close to roads for easy access; both sites have since been absorbed by suburban development.

Figures 2 and 3 show moist scrub in areas of low slope. The boundary between scrub and woodland was quite sharp at Site B (Fig. 3) but less clearly defined at Site A. Grids at Site A were laid 40m apart in typical moist scrub and woodland, whereas the grid at Site B traversed the abrupt shrub-tree junction.

Methods

Sampling Technique

To sample the vegetation at each site, a grid of rectangular quadrats was used. In dense vegetation, it is easier to count individual plants across the narrow width of a rectangle than in squares and, as Clapham (1932) showed, they may estimate density of plants with less variance than square quadrats of the same area (see Pidgeon and Ashby 1940).

Tapes were laid in parallel lines 15 feet (4.6m) apart across each site. Every 30 feet

(9.1m) along the tapes, and for 3 feet (0.9m) to one side, the numbers of individual plants of each species were counted. In this way, data were collected at each site for rows of contiguous quadrats ($8.3m^2$) arranged in columns 12 feet (3.7m) apart (see Fig. 4A).

Fig. 2. Moist scrub at Site A, East Gordon, with dry scrub on the ridge. (Photograph: I.M. Pidgeon, 1941).

Fig. 3. Abrupt junction between moist scrub and woodland at Site B, Elanora Heights. (Photograph: I.M. Pidgeon, 1941).

Isonome Mapping Technique

In each quadrat, the number of individual plants of each species was totalled and the relative density (relative abundance or importance value) was calculated as a percentage (e.g. 40 individuals of a species out of a total of 200 plants in the quadrat represent a frequency of 20%). The percentage frequencies for individual species in every quadrat can then be plotted on separate maps of the site, drawn to scale (Fig. 4A).

For each species, the variation in its relative density across the grid was mapped by lines drawn to connect areas with the same percentage values, in the same way as contour maps are constructed. These lines, termed 'isonomes' (from *iso*, equal, and *nome*, distribution) show the pattern of distribution for that species over the site, with one or more centres of high relative density emerging (Fig. 4B). The method of construction for an isonome map is fully explained in Results: Site A, Moist Scrub. By superimposing isonome maps for all species in sufficient abundance to generate discernible patterns, a composite pattern of species distribution over the area may be obtained.

The patterns in the isonome maps are obviously dependent on (a) quadrat size and spacing (how these are chosen for a particular type of vegetation is explored in the Discussion) and (b) variation in density of a given species over the grid.

Results

Isonome maps were prepared (in 1941) for twenty-three species selected to illustrate various features of the floristic analysis of mainly shrubby species (Table 1 and Figs. 4-9). Overall, one hundred and ten species were recorded (see Appendix). Some species were restricted to moist scrub, others to woodland, while a third group was common to both (see Table 2).

Table 1

Species represented in isonome maps and density per $85m^2$.

* denotes the site and vegetation type of species represented in Figs. 4-9, *x* denotes less than 1 per $85m^2$, (S) seedlings.

Species	SITE A Moist Scrub	SITE A Woodland	SITE B Moist Scrub	SITE B Woodland
Actinotus minor (Sm.) DC.	21	77*	100	20
Angophora hispida (Sm.) Blaxell	27	16	60*	3
Baeckea diosmifolia Rudge	236*	2	22	
Banksia ericifolia L.f. *var. ericifolia*	15	9	196*	22*
B. serrata L.f.		28*	9*	70*
Dillwynia floribunda Sm.			*x*	75*
D. retorta (Wendl) Druce		49*	3	44
Epacris microphylla R.Br.	49*	1		1
E. pulchella Cav.		29	60*	90*
Eucalyptus gummifera (Sol. ex Gaertn.) Hochr.		15*	5(S)	19
Grevillea sericea (Sm.) R.Br.		12	3	37*
G. speciosa (Knight) McGillivray	11		62*	1
Hakea teretifolia (Salisb.) J. Britten	160*	12*	238*	39*
Kunzea capitata Reichb.	673*	19*	246*	14*
Leptospermum trinervium (Sm.) J. Thompson	40*	31	9	38
L. squarrosum Gaertner	566*	15*	86	20
Leucopogon microphyllus R.Br.	85*	6*	90	13
Micrantheum ericoides Desf.	1	218*		29
Petrophile pulchella (Schrad.) R.Br.	235*	204*	98	74
Pimelea linifolia Sm.			25(S)	273*
Pultenaea elliptica Sm.	2	8	125*	48*
P. daphnoides Wendl.		27*		
P. retusa Sm.				16*

TABLE 2

Species restricted to moist scrub, woodland, and common to both excluding densities of 5 or less per 85m^2.
A & B denote the presence of species at either or both sites.
For common species, (S) denotes higher densities in moist scrub, (W) in woodland.
* denotes seedlings or young plants recorded in moist scrub.
Authorities for binomials as in Harden (ed.) Flora of N.S.W. Vols. 1-4.

	SITES			SITES	
MOIST SCRUB					
Allocasuarina distyla	A		*Gompholobium minus*		B
Aotus ericoides	A	B	*Grevillea speciosa*	A	B
Baeckea densifolia	A		*Hakea sericea*		B
B. diosmifolia	A	B	*Isopogon anethifolius*		B
B. imbricata	A	B	*Leucopogon esquamatus*	A	B
Bauera rubiodes		B	*Persoonia lanceolata*	A	B
Conospermum ericifolium	A		*Phyllota phylicoides*		B
Drosera peltata	A	B	*Woollsia pungens*	A	
Epacris microphylia	A				
WOODLAND					
Acacia longissima		B	*Lomandra glauca*	A	
Adiantum sp.	A	B	*Lomatia silaifolia*	A	B
Billardieria scandens	A		*Micrantheum ericoides*	A	B
Boronia ledifolia		B	*Monotoca scoparia*		B
Conospermum longifolium		B	*Patersonia glabrata*		B
Dillwynia floribunda		B	*Platysace linearifolia*	A	B
D. retorta	A	B	*Poranthera corymbosa*		B
Eucalyptus gummifera	A	B*	*Pultenaea daphnoides*	A	
E. haemastoma	A	B*	*P. retusa*		B
Gompholoblum virgatum		B	*Ricinocarpus pinifolius*		B
Goodenia stelligera	A		*Styphelia viridis*		B
Grevellea sericea	A	B	*Tetratheca ericifolia*		B
Hakea propinqua	A	B	*Xanthosia pilosa*		B
Hibbertia aspera	A	B	*X. tridentata*	A	B
Lasiopetalum ferrugineum		B			
COMMON					
Actinotus minor	A	B	*H. teretifolia*	A	B (S)
Angophora hispida	A	B (S)	*Hemigenia purpurea*		B
Banksia ericifolia	A	B (S)	*Kunzea capitata*	A	B (S)
B. oblongifolia		B (S)	*Lambertia formosa*		B
B. serrata	A	B (W)	*Leptospermum squarrosum*	A	B (S)
Boronia pinnata		B	*L. trinervium*	A	B
Bossiaea heterophylia	A	B (W)	*Leucopogon microphyllus*	A	B (S)
B. scolopendria	A		*Petrophile pulchella*	A	B
Comesperma ericinum		B	*Pimelea linifolia*		B* (W)
Epacris pulchella	A	B (W)	*Pultenaea elliptica*	A	B (S)
Hakea dactyloides	A	B (S)	*Xanthorrhoea resinifera*	A	B (W)

Site A: Moist Scrub

Figures 4A and 4B illustrate the method of construction of the isonome map for *Leptospermum trinervium*, one of the eight most abundant shrubs in moist scrub (Table 1, Site A). The grid map (to scale) in Fig. 4A shows relative densities of *L. trinervium* in each quadrat. Using the same principle as in contour mapping, 5% intervals were used to draw lines (isonomes) around these quadrats enclosing relative densities from 30% to 5% (interpolation of isonomes between two recorded frequencies is routine). In other parts of the grid, relative densities from 8% and 4% (column 1, rows 1 and 2) and 5% (column 2, row 4) enabled additional 5% isonomes to be drawn. In column 7, row 2, the quadrat with 11% relative density was circumscribed by 10% and 5% isonomes, as the flanking quadrats were 1%. The 3% isonome circumscribes all quadrats with relative densities from 3% to 5%, and excludes quadrats with lesser values or no presence. Construction of isonomes is, of course, discretionary, but consistent when done by the same person.

Isonome maps of the vegetation at this site show various levels of complexity. The

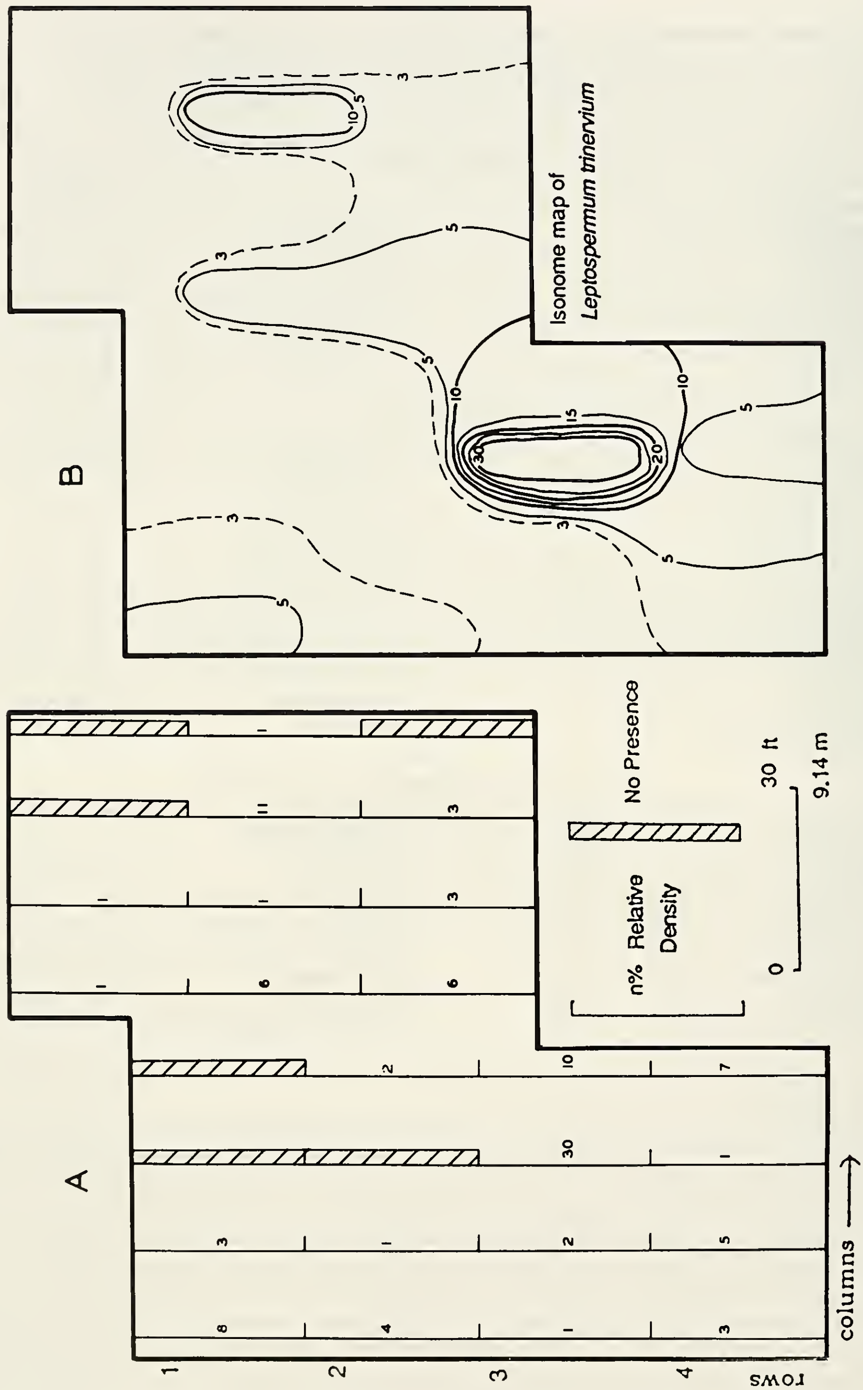

Fig. 4A, B. Method of construction of isonome map for *Leptospermum trinervium,* one of the eight co-dominant shrubs at Site A in moist scrub. A: Plan to scale of the grid; relative densities shown as percentages in each quadrat. B: Isonomes with intervals 5%, and 3% (broken line) drawn as contours from data in A. (See text, Results).

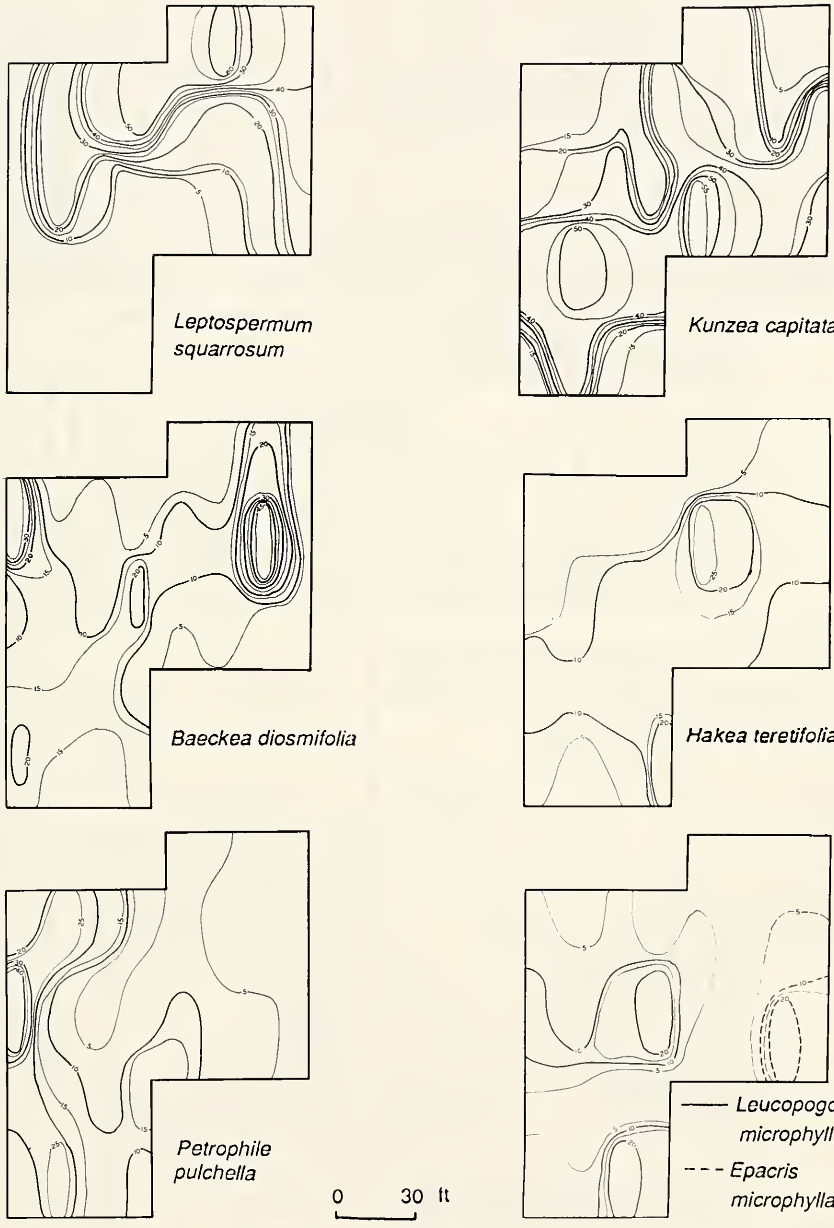

Fig. 5. Site A, scrub: Isonome maps (intervals 5%) for the other seven co-dominant shrubs in moist scrub, Site A. Centres of high relative density are: *Leptospermum* 60%; *Kunzea* 55% 50%; *Baeckea* 45% 35% 20% 20%; *Petrophile* 40% 25%; *Hakea* 25% 20%; *Leucopogon* 20% 20%; *Epacris* 20%.

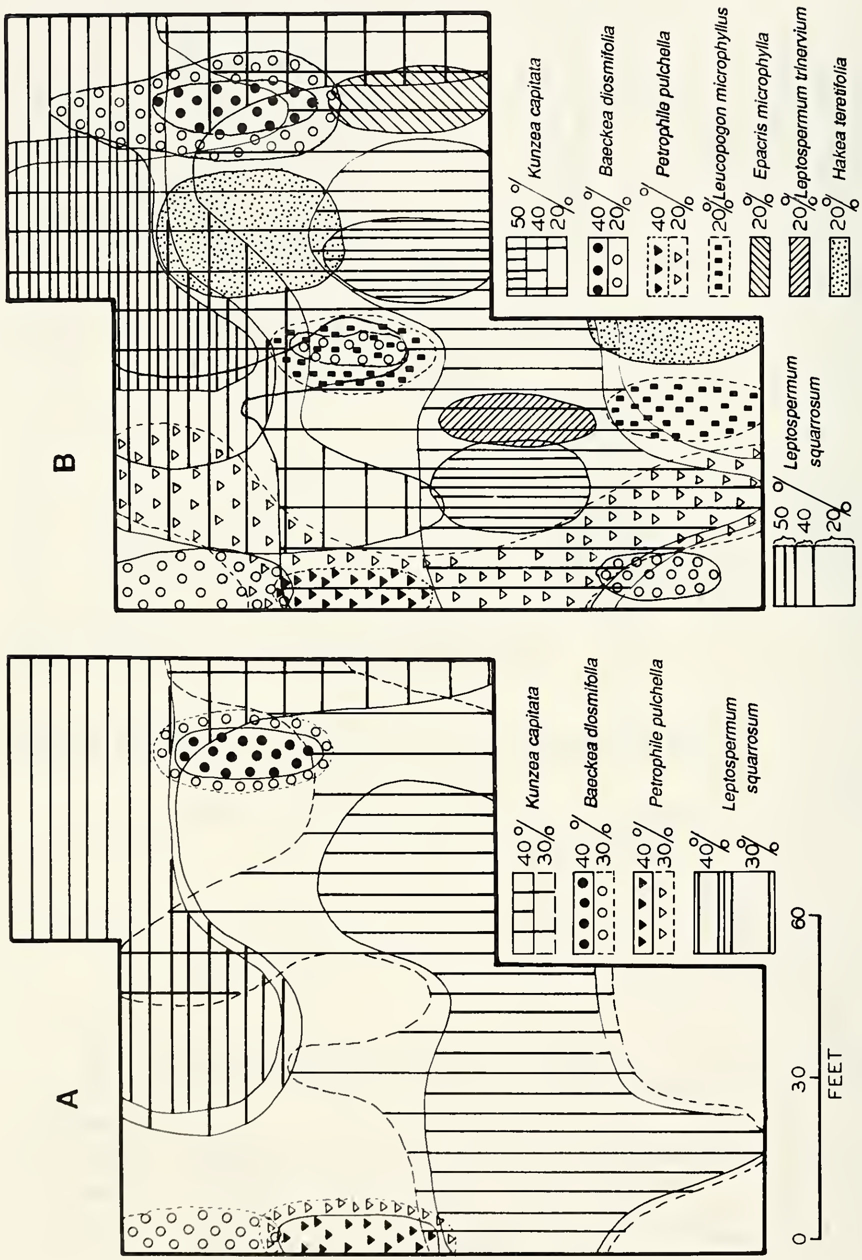

Fig. 6A, B. Patterns of distribution for shrubs in moist scrub, Site A, obtained by superimposing high value isonomes from maps of species in Fig. 4B and Fig. 5. A: Integrity of all high centres exceeding 40%, with small amount of overlap for 30% isonomes in the four most abundant shrubs. B: Mosaic obtained by superimposing isonomes of 20% or more for the eight co-dominant shrubs.

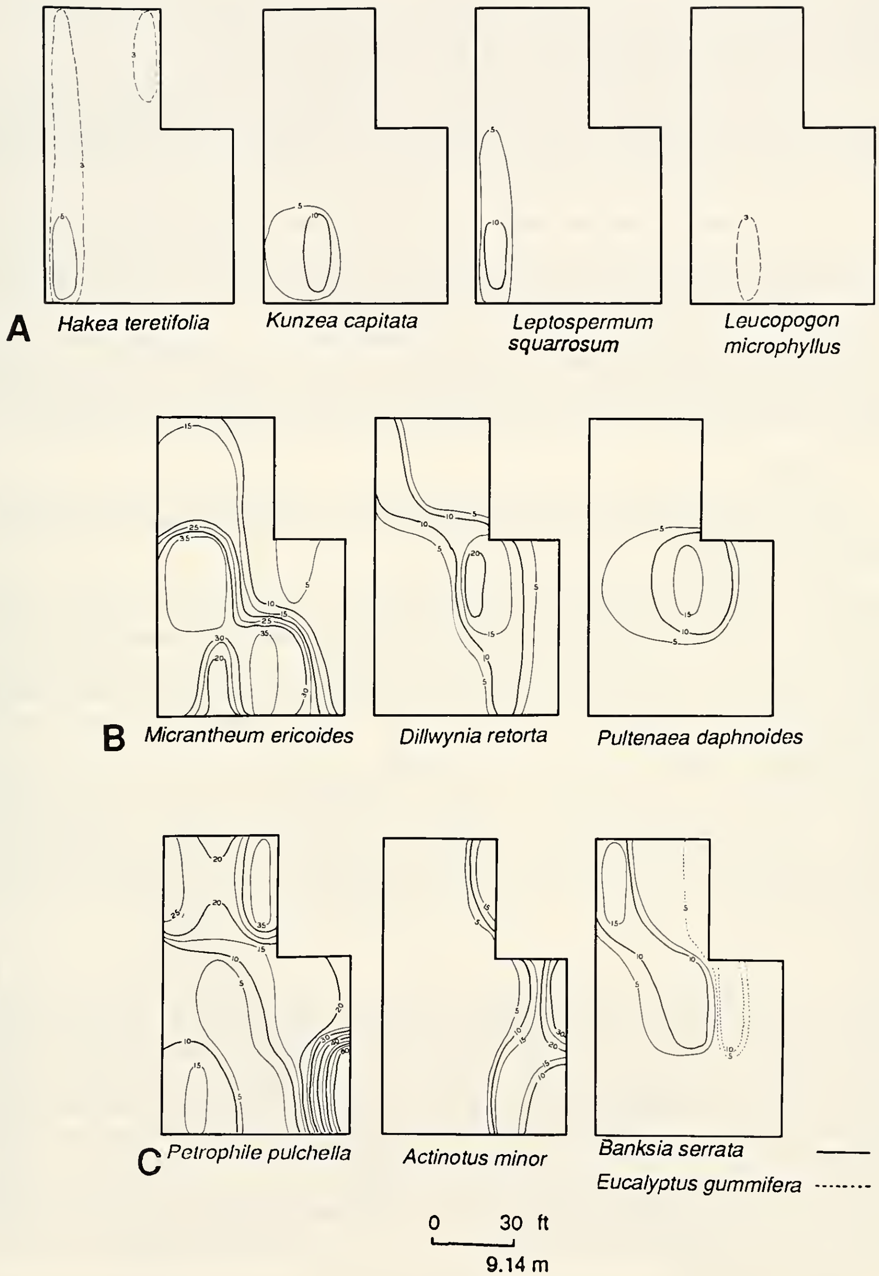

Fig. 7. Site A, woodland: isonome maps for eleven species with different patterns of distribution (see text). 7A: Four scrub species with restricted distribution of *Hakea* 5% 3%; *Kunzea* and *Leptospermum* 10% 5%; *Leucopogon* 3%. 7B: Three woodland shrubs with decreasing centres of relative density: *Micrantheum* 35% 35%; *Dillwynia* 20%; *Pultenaea* 15%. 7C: Two species occurring in scrub and woodland; centres of relative density are: *Petrophile* 60% 35%, *Actinotus* 30% 10%; and two species in the tree stratum: *Banksia* 15%; *Eucalyptus* 10%.

isonome map for *L. trinervium* is a simple pattern of distribution, with two centres of high frequency (30% and 10%) . Isonome maps (Fig. 5) for the other seven shrubs with the highest densities (Table 1), show mostly complex patterns which have several centres of high relative density varying from 60% to 20% (see legend, Fig. 5).

Although *Hakea teretifolia* appeared to be the dominant shrub at both sites in moist scrub, at Site A its density was significantly less than that of *Kunzea capitata* and *Leptospermum squarrosum* (see Table 1). However, as recorded in the thesis, only 10% (approx) of the population of *H. teretifolia* was less than 30cm high, whereas 50% (approx) of the population of both *K. capitata* and *L. squarrosum* was in this category.

By superimposing isonome maps for the eight shrub species (Figs. 4B and 5), the composite pattern over the whole area (1112-m^2) may be examined. Figure 6B, showing relative densities of 20% and above, reveals a complex 'social' structure in which the centres of high relative density for the various species form a mosaic, around the margins of which there is overlapping of the lower-value isonomes.

From the method of construction, it is clear that the collective number of relative densities cannot exceed 100% in any one place. The integrity of high centres greater than 40% and the small amount of overlap for isonomes of 30% are illustrated by Fig. 6A.

Site A: Woodland

In 500-m^2 of the adjacent *Eucalyptus gummifera — E. haemastoma* woodland, isonome maps (Fig. 7) were selected for eleven species with varying density (Table 1) and different patterns of distribution.

Four shrub species *Hakea teretifolia, Kunzea capitata, Leptospermum squarrosum* and *Leucopogon microphyllus* (Fig. 7A) that were abundant in moist scrub but had low densities in woodland (Table 1), show restricted patterns of low-frequency isonomes (Fig. 7A). This contrasts with the complex isonome maps for these same species in moist scrub (Fig. 5). Three shrub species restricted to woodland (Table 2), *Micrantheum ericoides, Dillwynia retorta* and *Pultenaea daphnoides* (Fig. 7B) with less complex patterns had corresponding decreasing densities (Table 1).

Petrophile pulchella (Fig. 7C) with similar high densities in scrub and woodland (Table 1) reveals a pattern similar in complexity to its isonome map in scrub (Fig. 5). In contrast, *Actinotus minor* (Fig. 7C), a herb also common to both habitats, but significantly less abundant than *P. pulchella* (Table 1) shows a simple pattern of distribution over part of the woodland. For two species in the tree canopy (Fig. 7C) the distribution of isonomes show no overlap.

Site B

At site B, the grid covered 933-m2 of moist scrub and 1510-m^2 of E*ucalyptus gummifera — E. haemastoma* woodland, with an abrupt tree boundary (Fig. 3). Isonome maps for twelve species of shrubs reveal various patterns of distribution (Figs. 8A, 8B, 9A, 9B).

Two species, *Hakea teretifolia* and *Kunzea capitata,* (Fig. 8A) with high densities (Table 1) and complex patterns in moist scrub, show restricted distribution in the adjoining woodland, as at Site A (Fig. 7A). Conversely, *Pimelea linifolia* (Fig. 8B) was restricted to woodland and occurred only at Site B where its isonome pattern is complex. Its occurrence in moist scrub was solely as seedlings (Table 1). *Epacris pulchella* (Fig. 8B), though present only in the woodland at Site A (Table 1) occurred in both scrub and woodland at Site B, where the high centres of distribution on each side of the tree boundary are linked by lower-value isonomes.

Pairs of species in three genera, *Grevillea* (Fig. 9A), *Banksia* and *Pultenaea* (Fig. 9B), have complementary patterns of distribution in scrub and woodland, with some overlapping: *G. sericea* into scrub, *B. ericifolia* and *P. ellipitica* into woodland. The isonomes for two species are abruptly terminated at the treeline, confining *Dillwynia floribunda* to woodland, and *Angophora hispida* to scrub (Fig. 9A).

DISCUSSION

In these field trials of the isonome mapping technique, the priority was to determine whether the selected size and spacing of the quadrats was appropriate for mapping isonomes in shrubland and woodland. Investigations at both sites were therefore limited to a floristic analysis. No soil samples (the obvious variable) were taken at this time. However, other field investigations by the author in similar areas indicated the importance of soils and drainage patterns in determining the two vegetation types: woodland and moist scrub.

Isonome Mapping Techniques

Based on relative abundances of the component species, the isonome method of analysis of vegetation uses density as the principal attribute with which to describe vegetation.

Isonome mapping seeks to display variation in patterns of distribution of individual species by mapping contours from the variation of their relative density in sampling units across the grid. The maps generated are dependent not only on the distribution and density of the indivuals of species mapped, but also on the spacing and size of the quadrats

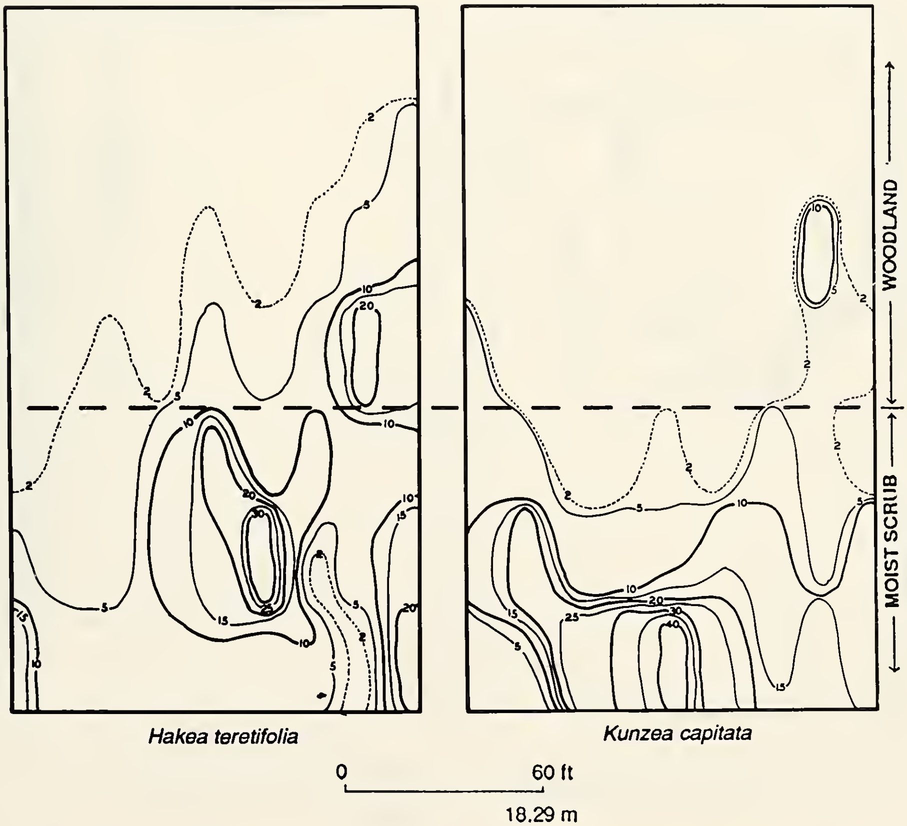

Fig. 8A Site B: isonome maps for two shrubs dominant in moist scrub (see text). Intervals 5%, with 2% boundaries (dotted lines). Centres of relative density are: *Hakea* 30% 20% 15% (scrub), 20% (woodland); *Kunzea* 40% (scrub), 10% (woodland).

used. Clearly, if the size of these is so small that few individuals of few species are included in each sample, then relative densities will vary greatly over short distances, and it would be difficult to map isonome contours that are meaningful. Conversely, if the quadrats are very large, variation in relative density of species will be discerned only at large scales.

The investigator has to choose the scales of variation that are of interest. In this case, interest was in variation of patterns of distribution in species, especially shrubs, between two structurally distinguishable types of vegetation: scrub and shrub-woodland. The area sampled in each had to be large enough to represent the range of variation in distribution of the common species in them, and the samples taken in them appropriately sized and spaced to explore that range of variation. The size of the samples, rectangular quadrats (9.1 x 0.9m), was large enough to contain individuals of a number of species and they were numerous enough and appropriately spaced to map isonome contours within the types of vegetation. The isonome maps produced thus reflected the variation in relative densities of species within the types of vegetation and allowed comparison of patterns of variation in relative abundances between them.

The quadrat size and spacing may be varied to suit the type of vegetation: the method was worked out on dense scrub vegetation (see Figs 2, 3). Other vegetation types

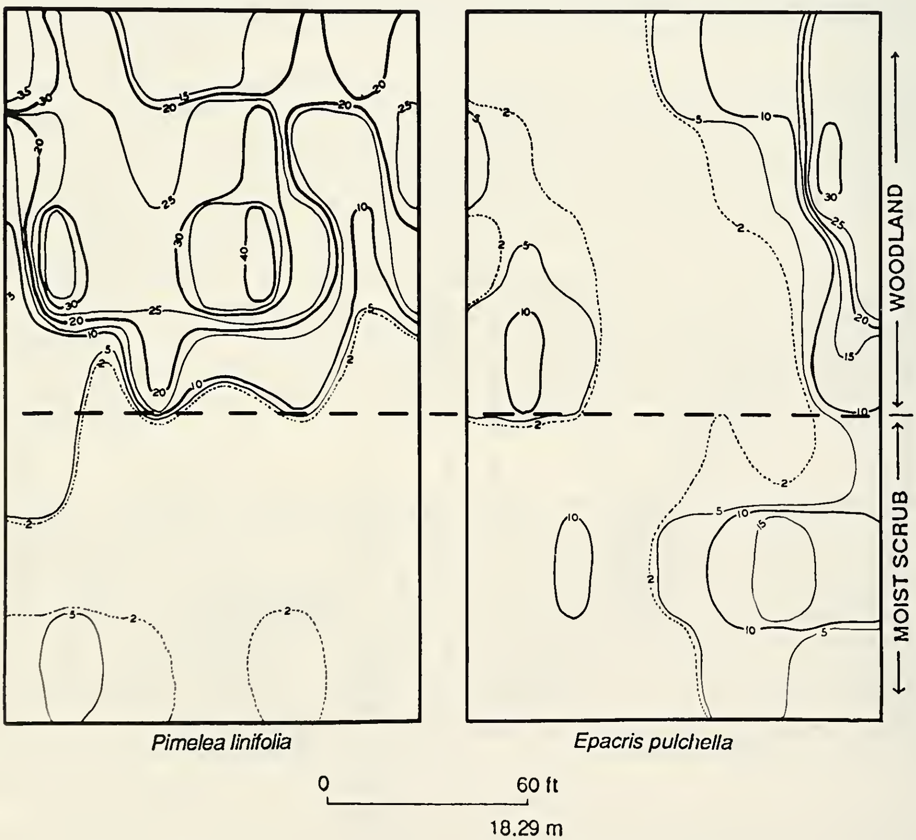

Fig. 8B Site B: ecotone boundaries for two shrubs (see text). Isonome intervals 5% with 2% boundaries (dotted lines). Centres of relative density are: *Pimelea* 40% 35% 30% 25% (woodland); *Epacris* 30% 10% (woodland), 15% (scrub).

may require quadrats of different dimensions. For sand dune vegetation (see Pidgeon, 1942) it was more appropriate to use sampling units of half the length (compared with scrub and woodland), to compensate for the spatial zonation of vegetation from fore-dune to hind-dune. In an investigation of grassland, it is very probable that the quadrats would need to be smaller and closer together than were used in this analysis.

A similar system of isonomes is obtained if absolute densities (actual numbers) instead of percentages (relative densities) of each species is plotted. Isonomes not calculated on a percentage basis have a limited application; they are not so useful when comparing relative densities of species, and cannot be used as in Fig. 6 for a composite pattern of the area (Pidgeon & Ashby, 1942).

It is generally more useful to eliminate variations in absolute density of the plant population over the area investigated by reducing figures to percentage cover of individual species. However, where there are considerable bare areas, e.g. on coastal dunes, or in arid regions, the vegetation cover may be expressed as percentage cover of total quadrat area; this also estimates at the same time the amount of the bare area. Percentage cover of each quadrat would also be estimated for stoloniferous grasses and for cloned species.

With distinct two-layered communities, it may be advantageous to collect the data from the separate strata, and construct two sets of isonome maps; where the ground layer is insignificant, it may be ignored altogether.

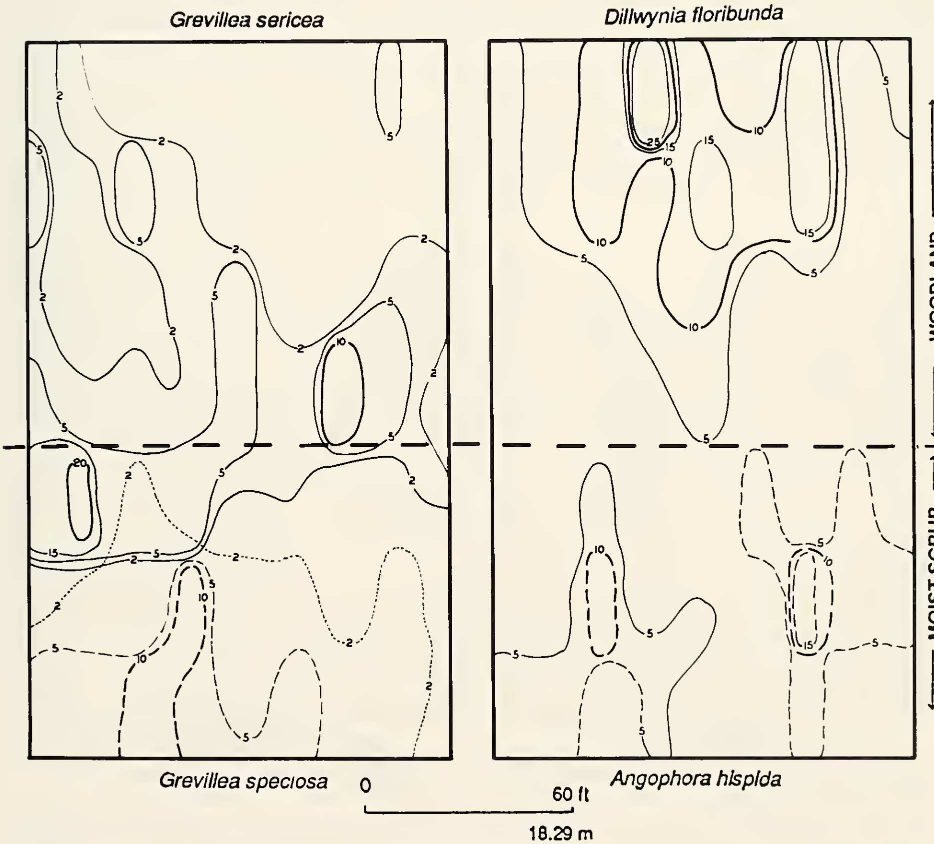

Fig. 9A Site B: ecotone boundaries for four shrubs (see text). Intervals of 5% with 2% boundaries for *Grevillea spp.* Centres of relative density shown: *G. sericea* 20% (scrub) 10% 5% (woodland); *G. speciosa* 10% (exclusive to scrub); *Dillwynia* 25% 15% 15% (exclusive to woodland); *Angophora* 15% 10% (exclusive to scrub).

The labour involved in counting individuals of several species in numerous samples limits isonome mapping to small areas of less than a hectare, more than sufficient to map patterns of distribution. With the assistance of about 20 second-year ecology students in 1941, the field recordings in this study were completed in one day at each site. The work involved in constructing isonome maps would be reduced by computer graphics.

Although random-sampling techniques are most frequently used in quantitative analysis, Buchanan and Humphreys (1980) also used a grid (of circular quadrats in columns and rows) traversing the sharp boundary between podzol and non-podzol soils at two sites on Hawkesbury sandstone, to analyse by modern techniques, the sudden floristic change which accompanies the change in soil type.

Patterns of variation in distribution and abundance of species

Tree seedlings which become established in moist scrub (see Appendix) during dry summer periods do not survive when the water table rises after prolonged wet periods. The lack of aeration affects their root systems, which penetrate deeper than the shrubby species. During a series of dry years, Buchanan (1980) also recorded, in dried swamps, the growth of Eucalypts to several metres, before the water table rose and killed them.

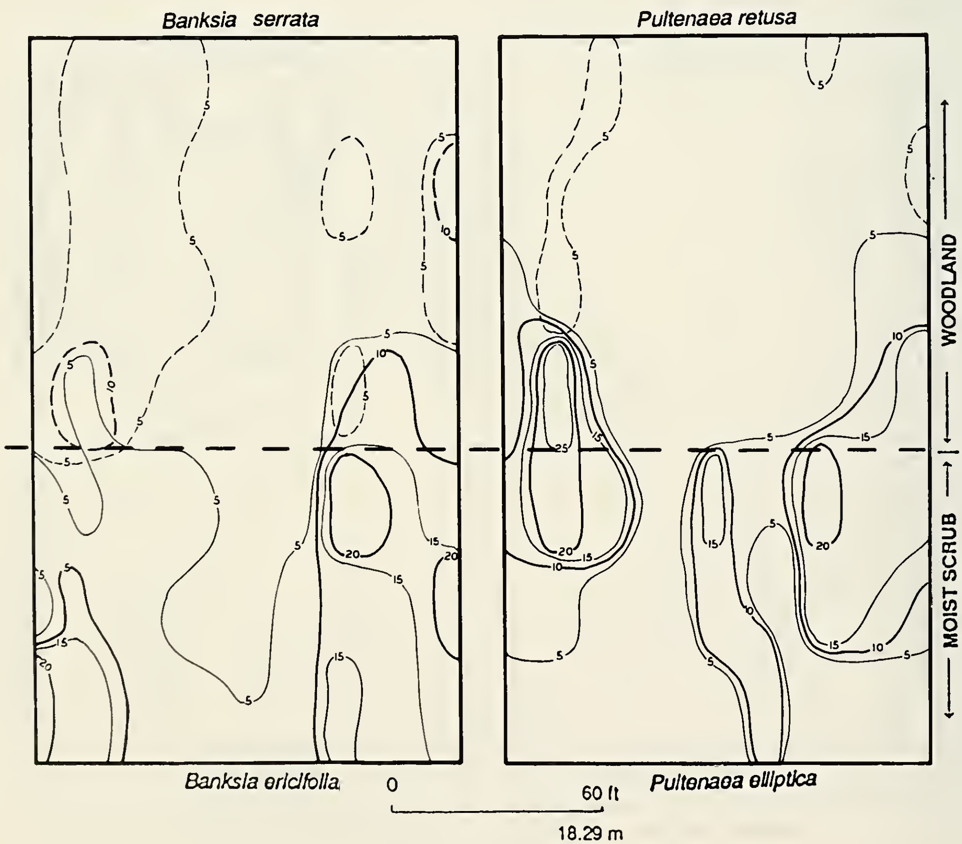

Fig. 9B. Site B: Distribution of four shrubs in relation to the ecotone; isonome intervals 5%. Centres of relative density are: *Banksia serrata* 10% 10% 5% 5% (exclusive to woodland); *B. ericifolia* 20% 20% 20%; *Pultenaea elliptica* 25% 20% 15%; *P. retusa* 5% 5%, 5% (exclusive to woodland).

In the distribution of species between scrub and woodland, there were consistent results across both sites; some species were restricted to woodland, some to moist scrub; others were in common to both vegetation types; in this third group, most had substantially higher densities in scrub or woodland (Table 2). With the more abundant species of shrub, isonome mapping illustrated variation in relative densities between woodland and moist scrub, again with a high degree of consistency between the two sites. Overall, the density of shrubs in scrub and woodland is in the approximate ratio of 2:1 at both sites (see Appendix).

Isonome mapping in this study revealed patterns of variation in abundance and distribution of species across the ecotones between woodland and moist scrub (Site B) that were not apparent even to the keen observer:

(1) The exact extent of the overlap for shrub species which intrude into woodland, or understorey shrubs which intrude into scrub

(2) Complementary patterns of distribution between pairs of species of the same genera that were precisely defined in scrub and woodland

(3) The abrupt termination, at the sharp shrub/tree ecotone of some species of shrub, exclusive to woodland or moist scrub

Differentiation in distribution and density of species may be related to spatial variation in soil or in the behaviour of fires.

Buchanan (1980) observed that, at abrupt ecotones of moist shrubland and woodland, an obvious change in understorey shrubs (not specified) coincided with an abrupt junction of the impervious sub-soil (less than 1m below the surface) with the well drained sandstone soil of the woodland; a more gradual change in the understorey shrubs takes place when the impervious layer thins or deepens beneath the trees. As the abundance of some species of understorey shrubs at Site B is closely associated with the abrupt ecotone (Figs. 8B, 9A) it may be inferred from Buchanan's observations that the junction between the impervious sub-soil of the scrub with woodland soil at Site B was also abrupt, as was assumed, but not verified in 1941.

Variations in vegetation on sandstone, related to variations in soil characteristics, have been observed by Pidgeon (1937, 1941), Siddiqi *et al.* (1972), Burrough *et al.* (1979) , Buchanan and Humphreys (1980) and noted by others, Thomas and Benson (1985), Outhred *et al.* (1985). Though no observations were made on the soils at Sites A and B, the differences between woodland and moist shrubland soils are generally well known, particularly the well-drained woodland soils in contrast to the temporary waterlogging characteristic of the moist scrub soils (Pidgeon 1938, Beadle 1962, Buchanan, 1980). The overall distribution and abundance of species between woodland and moist scrub and the exclusive presence (or preference) for a particular habitat (Table 2) is more likely to be related to spatial variation in soils, than to spatial variation in the behaviour of fires.

There was no evidence of recent fires at either site, confirmed by the dominance in moist scrub of shrubs killed by fire (Table 1). Fire is probably the main factor in determining composition and abundance of obligate-seeder species, largely controlled by fire frequency and inter-fire periods (see Thomas & Benson, 1985; Benson, 1985; and Keith in Press). Recent research into population dynamics, starting with such observations, has been developed in studies of individual species (Bradstock & Myerscough, 1981; Auld, 1986). Isonome mapping provides an avenue for relating these population-level studies to the sociology of communities which an experienced ecologist can interpret, often more rapidly than from computer-analysis.

The restricted, low-value isonomes of obligate-seeder shrubs in woodland, abundant in scrub (Figs. 7A, 8A), could be considered as 'relics' of a pyric succession. Alternatively, they may be due to shading out by taller growing species in the absence of fire.

In summary, isonome maps presented in this floristic analysis of moist scrub and woodland have revealed, for the first time in graphic detail, the structure, sociology, distribution and abundance of species in these sandstone communities, and supported some observations by other researchers:

(i) The association between high density of occurrence and vegetation type has been confirmed.
(ii) Patterns of occurrence and density across ecotones have been revealed.
(iii) Patterns of positive association, not previously apparent, have been discovered.
(iv) Specific patterns i.e. relics in woodland of some obligate - seeder woody shrubs, abundant in adjacent scrub, have generated an hypothesis of temporal change operating at a small scale.

In an age when sophisticated computer-based statistical techniques are used to analyse the structure of plant communities, the simplicity of isonome mapping, in association with investigation of micro-environmental factors, offers some advantages which are worth further exploration.

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APPENDIX

Species and densities per 85m. sq. recorded in quantitative analysis of adjacent areas f moist scrub and woodland, Sites A and B.

x = recorded but less than 1 per 85 m. sq., + = cloned species not estimated, s = seedlings only
Authorities for the binomials: Harden, Ed. (1990-93), Vols. 1-4, Flora of New South Wales

Species	SITE A Moist Scrub	SITE A Woodland	SITE B Moist Scrub	SITE B Woodland
Allocasuarina distyla	19		1	
Acacia brownii		2		
A. longissima				15
A. myrtifolia				4
A. suaveolens	5	2	1	x
Actinotus minor	21	77	100	20
Adiantum sp.	3	31	1	7
Angophora hispida	27	16	60	3
Aotus ericoides	16		78	x
Baeckea brevifolia	2			
B. densifolia	8			
B. diosmifolia	236	2	22	
B. imbricata	36	1	7	
Banksia ericifolia var. ericifolia	15	9	196	22
B. oblongifolia	3	2	39	9
B. marginata		5		
B. serrata		28	9s	70
B. spinulosa	3	5		5
Bauera rubioides			75	5
Billardieria scandens	1	11		x
Boronia ledifolia			5	30
B. pinnata		2	19	12
Bossiaea heterophylla	1	42	7	27
B. scolopendria	6	17	3	1
Cassytha glabella	x			
Caustis flexuosa	x			
Ceratopetalum gummiferum				x
Choretrum candollei				x
Comesperma ericinum			23	18
Conospermum ericifolium	8			
C. longifolium				14
Dampiera stricta			1	4
Darwinia fasicularis	1		3	
Dianella caerulea				2
D. laevis	1	3		
Dillwynia retorta		49	3	44
D. floribunda			x	75
Drosera peltata	25	3	7	x
Epacris microphylla	49	1		1
E. pulchella		29	60	90
Eucalyptus eugenioides		1		
E. gummifera		15	5s	19
E. haemastoma	1s	5	6s	6
E. racemosa				x
E. sieberi				x
Gompholobium virgatum			1	16
G. minus			8	
Goodenia stelligera	3	25	3	1
Gonocarpus teucrioides		2		1
Grevillea buxifolia	3	4		2
G. speciosa	11		62	1
G. sericea		12	3	37
Hakea dactyloides	11	2	53	8
H. propinqua		5		8
H. sericea			13	
H. teretifolia	160	12	238	39
Hemigenia purpurea	1		10	6
Hibbertia aspera		8		24

Species	SITE A Moist Scrub	SITE A Woodland	SITE B Moist Scrub	SITE B Woodland
H. riparia	1		2	1
Isopogon anethifolius	4		24	3
Kunzea capitata	673	19	246	14
Lambertia formosa		1	17	18
Lasiopetalum ferrugineum			x	16
Lepidosperma sp.		11	8	2
L. laterale	1			
Leptospermum arachnoides	x	1		
L. squarrosum	566	15	86	20
L. trinervium	40	31	9	38
Leucopogon appressus		3		
L. esquamatus	15	5	98	2
L. microphyllus	85	6	90	13
Lindsaea microphylla		3	x	x
Lomandra sp.				+
Lomandra sp.			+	+
L. glauca	+	+		
Lomatia silaifolia		12		6
Micrantheum ericoides	1	218		29
Mirbelia rubiifolia	1		5	
Monotoca scoparia			1	11
Olax stricta				2
Patersonia glabrata			1	35
Persoonia hirsuta		2		
P. lanceolata	9	2	16	3
P. mollis			1	
P. levis			4	4
Petrophile pulchella	235	204	98	74
Philotheca salsolifolia			1	
Phyllota phylicoides			59	
Pimelea linifolia			25s	273
Platylobium formosum				2
Platysace linearifolia	1	25	1	13
Poranthera corymbosa				10
Pteridium esculentum				1
Pultenaea elliptica	2	8	125	48
P. daphnoides		27		
P. retusa				16
P. stipularis		2		
Restio fastigiatus	+			
Ricinocarpus pinifolius			1	6
Stylidium graminifolium	5		1	
Styphelia tubiflora		2		
S. viridis			4	9
Telopea speciosissima				2
Tetratheca ericifolia	1		2	8
Woollsia pungens	13			1
Xanthorrhoea resinosa	7	12	8	41
Xanthosia pilosa				20
X. tridentata		7	3	12
Xylomelum pyriforme				4
Zieria laevigata	5		1	